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Cousin Marriage and Population Structure*

WE HAVE ALL heard from our early youth about the dangers of cousin marriage. Most of us have probably associated it with the prohibitions of primitive society or perhaps of the Christian Churches. You may not all know how erratic, how various, these prohibitions are.

Historical Background

In the eleventh century when the Catholic Church reached the peak of its power it set out to prohibit cousin marriage between any kin nearer than what was called the seventh degree of kinship. Furthermore this seventh degree was taken to mean that there must be no common ancestor within seven generations. It was on this ground that William the Conqueror erred when he married Matilda, his fourth or fifth cousin, and that he and she, in order to expiate their sin, built the Abbaye aux Hommes and the Abbaye aux Dames at Caen. Similarly the Conqueror's son, Henry I, was forbidden to marry one of his bastard daughters to the Earl of Surrey on the ground that they were sixth cousins.

The Nineteenth Century

From these remote and ill-founded rules we can come to recent times and consider what the attitude of scientists has been to this problem. Charles Darwin was interested in it, quite apart from his general ideas, owing to the fact that he had married a first cousin himself. But the crisis of his interest came when he was studying the mechanisms of cross-fertilization in flowers, those mechanisms which we now understand in such great detail. He wanted to know why these mechanisms were so widespread. The conclusion he came to was that the progeny of cross breeding were more vigorous than the progeny of inbreeding, and this property had favoured the development of cross-breeding mechanisms in the course of evolution.

This view can no longer be sustained. It could not be sustained by his own son, George Darwin, who inquired about the results of cousin marriage in our own population. He tried to find out whether the progeny of cousin marriages were less numerous or less viable, and he failed to get any decisive evidence of a difference between the two. It was then, in 1876, that Darwin persuaded Lubbock to try to introduce an inquiry into the census as to whether marriages were between first cousins or not, but the House of Commons rejected the proposal.

Garrod's Study of Alkaptonuria

The next step in the study of cousin marriage brings us into our own century; it is the study by Garrod in 1902, of the disease *alkaptonuria*, which occurs in about one in a million of our own population. Garrod was led to inquire into this disease by the early work of Bateson on Mendelism. The inheritance of this condition suggested a Mendelian recessive situation. Now cousin marriages, as we know, occur in the population in about 1 per cent and non-cousin marriages in 99 per cent. But Garrod found that from these cousin marriages came 33 per cent of all the alkaptonurics; only 67 per cent came from all the non-cousin marriages. About thirty-three times as many came from the cousin marriages as should do. How was this to be explained?

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If one in a million people showed this disease it would mean one in a thousand of the chromosomes responsible for the disease were determining that recessive character. If the alkaptonuria condition is that of the pure recessive *aa* it will arise in the population from crossing two heterozygotes. If *a* is present in the relevant chromosome pairs of the population to the extent of one in a thousand, heterozygotes will be present in one in five hundred individuals. But cousins should have on the average one-eighth of their chromosomes and genes in common. So if you are a heterozygote the probability is that your spouse, who is your first cousin, instead of having a one in five hundred chance of being hetero-alkaptonuric will have one-eighth of a chance. Instead of being one in two hundred and fifty thousand the chance will be one in four thousand. This was the explanation Garrod gave for the very high frequency of alkaptonuria amongst the progeny of cousin marriages.

This principle has been widely used, and in a preliminary and provisional sense well used, for the study of Mendelian recessive conditions in our population. But in an ultimate sense there are objections to that use. These I am now going to consider because they have a great deal to do with the study of cousin marriage. What assumptions have been made in talking about the one in five hundred or the one in eight? We have assumed that our population is composed of individuals who are mating at random, and that this is the difference between the non-cousin marriage where the mating is at random and the cousin marriage where the mating is not random. The fact that cousin marriages occurred fifty years ago in 1 per cent of the population shows that that assumption is not exactly right.

Social Groups and Inbreeding

In fact, of course, our population is composed of groups. If you like, for convenience, you can say these are groups within which mating is at random. But these groups are of all sizes, small and large. If you have a very large group it might be equivalent to having random mating amongst the whole population. But if it is a small group of only half a dozen families all marriages are first cousin marriages, and the distinction between non-cousin marriage and cousin marriage has disappeared. So the situation is vastly more complicated than Garrod's classical assumption would lead us to suppose.

If, in fact, we have groups within which mating is at random, but there are small groups in which there is close inbreeding and large groups in which there is little inbreeding, we must find out a good deal about the structure of our society before we investigate cousin marriage. We must find out not only whether the marriage is between first cousins, but also whether the parents or grandparents of the cousin marriage were themselves likely to be closely related or unrelated.

Let us now consider a contrast of method. In Mendel's experiments, he began with pure lines which had been inbred. The Mendelian system was one in which there was inbreeding for an indefinite number of generations, and this was followed by his critical act of outbreeding, to give the F1; this was followed again by inbreeding for an indefinite number of generations. In the cousin marriage which classical genetics considers, there is outbreeding for an indefinite number of generations, followed by a critical act of inbreeding, the cousin marriage; this again is followed by an indefinite number of generations of outbreeding. In other words, you are dealing with a reversal of the Mendelian experimental situation, a reversal provided for us by the customs of our society. But we have to be quite sure that it is indeed a reversal and how much of a reversal.

You might say that is an absurdly difficult task to set ourselves, we simply have not the records with which to do it. I am attempting to show that, in fact, we can construct our situation; we can obtain our records. Look at the question from another point of view. Garrod, and those who studied Mendelian inheritance, were not dealing for the most part with the fundamental properties that interest us. They were not dealing with the fundamental properties of viability, fertility or intelligence. Those are not for the most part subject to the simple Mendelian inheritance which is capable of being investigated on their lines. They are not necessarily due to genes which operate in the same way. They are often governed by gene arrangements in which the interaction between different genes is as import-

ant as the interaction between the forms of the same genes. All these systems in human breeding are undefined, unexamined, unanalyzed, and so far beyond our correct analysis.

Galton and Hereditary Fertility

Now there was one man who did think of inheritance in this integrated and non-analytical sense, and who did approach this problem of fertility which escapes Mendelian analysis. That was Galton. His method he describes in a casual way in his *Hereditary Genius*. The question arises in relation to the fertility of heiresses and the extinction of peerages.

I mention one historical fact which does not seem to be realized. It was that his grandfather, Erasmus Darwin, had asked the same question and had given the same answer that he, Galton gave. Erasmus Darwin asked why heiresses were so often infertile and peerages became extinct. He suggested that the mothers of heiresses, having no sons and fertility being hereditary, the peeresses who were heiresses would have fewer children than the average population; and that is how peerages became extinct. I am sure Galton was unaware of what his grandfather had done. He says, "This does not seem to have occurred to anybody before."

The actual records Galton used show one odd point. Working from Burke's *Peerage* he said 100 heiresses had 208 sons and 206 daughters, and 100 non-heiresses had 336 sons and 284 daughters. I cannot understand where those fifty or so daughters of non-heiresses got lost. He does not say anything about it himself and I think our statisticians, disciples of Galton, should do something to explain how he overlooked this irregularity. Between heiresses and non-heiresses, however, we see a great difference. The non-heiresses are much the more fertile. In fact, too much. There should not be, in my opinion, quite that enormous difference. The reason for it I shall try to explain later.

This kind of study was repeated later by Karl Pearson, and his results have been re-examined by Fisher. They show a regular difference between the women according to the size of the family from which they come. I might give a short résumé and examples, taking the numbers of progeny in Pearson and Lee's results of 1899. Where the mother came from a family of one, the average number of children was 2·97; from a family of four, average number of children 3·41; from a family of eight, 4·07; where it was in the group from twelve to fifteen the number of progeny was 6·44.

This not merely shows that fertility in men or women is hereditary; it also shows something which many people nowadays would strongly repudiate. They would say the number of children people have is a matter of their own free will; it must be something outside genetical control. The assumption Galton and Pearson made was that there was a strong genetic component in the resultant fertility. We do not need to ask whether it was due to physical sterility or lack of desire for children or incapacity to have them, the result shows the action of a genetic component popularly called heredity.

Methods used for Present Investigation

It is on the assumption that this principle operates that I have been conducting my own investigations. One word about the methods I used. In the first place, I asked the academic world of Oxford, through the *Oxford Magazine*, for information about the fertility of the progenies of cousin marriages: not the number of children produced by cousin marriages but the number of children produced by the children, and the grandchildren. On the basis of the small results of this inquiry I was able, through the *Observer* in London, to appeal to a much larger public and get much larger samples of the population of grandchildren of cousin marriages. Armed with this information I was able to make the inquiry wider still. Through a Swiss multilingual publication, *Triangle*, I was able to appeal to people all over the world for data on cousin marriages, giving more rigorous requirements.

The results of all three inquiries are combined in what I will tell you now. The observations came from scattered parts of the world—Sweden, Holland, Austria, Australia, United States, Canada, and so on. From this I got a representative notion of what happens in our population. I found there were families in which cousin marriage occurred generation after generation, or sometimes in alternate generations going back

a dozen generations to the beginning of the seventeenth century. There were other families in which there was no evidence of any cousin marriage previously and then suddenly a cousin marriage occurred. Again it was necessary to make a distinction between different religious or social groups. In dealing with a family of white Bermudians, the white population of Bermuda being exceedingly small, that population is likely to be inbred; the same applies in a small religious community like the Irish Quakers.

Dealing with a Jewish population in Hohenzollern we know it is inbred. We know 15 per cent of the population marry first cousins and the probability is they have done so for many generations. On the other hand, with Church of England people, middle class, well educated, who have no knowledge of any cousin marriage in the family, the probability is that we are dealing with an outbred population. This can be confirmed by exhaustive information of ancestry. Studying the matter in that way I got a general indication as to the way in which populations breed.

Inbred Communities

For example, with the Mennonites, a group of Anabaptists, observance of the delicate minutiae of baptismal regulation has given us the strictest of inbreeding systems. The Mennonites were founded in 1528 in Germany. Being pacifists, they have found their position increasingly uncomfortable in all parts of the world. When a war comes and there is conscription the Mennonites are pushed out. They are an agricultural community who live in small settlements, and marriage occurs within those settlements, usually of less than a hundred families. Almost everybody has to marry a first or second cousin. As the group grows it splits up into smaller groups which migrate into new territories, thus continually forming new inbred communities.

I was able to get a pedigree from Vienna of the descendants of Moses Göring, who married in 1785. I have only the descendants in the male line. The female line, not carrying the name, is a matter of general indifference to people who maintain pedigrees. Moses Göring in the male line had four sons, nine grandsons, twenty-nine great-grandsons—these all surviving to maturity —and ninety great-great-grandsons. Assuming that the female line was equally fertile, we have to multiply those figures by 2, 4, 8 and 16, giving a total of 1,440 great-great-grandchildren. An average of six children per marriage reach maturity.

According to studies made in South Dakota, the number of Mennonite immigrants which moved there in 1874 was 300. In 1950 there were 9,000 descendants of those 300. They occasionally lose a member who cannot face the rigors of the system and deserts to the outer world; but they never marry outside and never gain from outside. Eaton and Mayer, who studied this population, found in these families at the present day an average of 10·9 children per marriage, reaching maturity. So far as I can make out, every child who reaches maturity gets married, and the number of children per marriage has slightly increased during the last three generations from 10·2 to 10·9. That I attribute to the fact that this is a communized or socialized system in which nobody needs to worry about the children being cared for if anything happens to the parents. The selective situation is biased in favour of the highest fertility; consequently the highest fertility is gradually being approached.

Here is a system giving perfect conditions for selection for fertility. Fertility is obviously hereditary and very high and is maintained with a system of close inbreeding in which cousin marriage does not reduce the fertility at all. On the contrary, sterility can arise only by genetic recombination and without outbreeding there is no recombination. That is the situation with the Mennonites, and I imagine it would be true with other stable inbreeding societies. Above all, it would be true of stable primitive tribal societies.

Cousin Marriage in an Outbred Society

Contrast this situation with the results of a cousin marriage in our own outbred society, in a family in which there had been very little previous inbreeding, the family of Charles Darwin. It was this family that first called my attention to the peculiar possibilities of the problem. Their dates are important owing to the

introduction of birth control and other social changes. Darwin was born in 1809. He married, in 1839, his first cousin, a year or two older than himself; and he died in 1882. The total number of children was ten; the number that survived to maturity seven; the number that married was six. The number of those marriages that had issue was three. This is a very different result from that found in the Mennonite community. But it is typical of our own outbreeding community, with the difference that the proportion that are with issue is smaller than average.

Take the grandchildren: the total is nine. Of these there were married eight, with issue seven. At this stage there begins a recovery: the proportion of marriages with issue is higher. The total number of great-grandchildren born is twenty-eight. Thus there is also a higher average frequency of children per marriage with issue than there was. Although the birth rate in the community has decreased, in that particular lineage it has increased. This single family is not in itself significant. But it was this family that put me on to considering the situation in families at large. It is an example of a cousin marriage with inbreeding occurring after outbreeding, and followed again by outbreeding.

Taking my results in general, I have separated the community, so far as I could, very roughly and arbitrarily and provisionally, in order to get some guidance, into inbred and outbred stocks. I give the summarized data: the cousin marriages in outbred families are contrasted with the cousin marriages in inbred families belonging to small religious groups and in families with previous cousin marriages authenticated. I give the children, the grandchildren and the great-grandchildren.

	COUSIN MARRIAGES		G. CHILDREN	GG. CHILDREN	INCREASE
Outbred	39	234	342	499	×2·1
Inbred	9	57	146	257	×4·5

In other words, the descendants have multiplied in the two generations by 2·1 and 4·5. This seemed to me a *prima facie* case for concluding the effect of cousin marriages was to depreciate the fertility of the progeny in families where there had been previous outbreeding. At the same time there was no evidence of such depreciation in the inbred families. The change in the breeding system had produced the depreciation.

Now I realized that the grounds on which one distinguishes between outbred and inbred families might be open to dispute, and it was desirable to get a more rigorous test of the differences between these two types of breeding system. The method of doing it was suggested to me by a grandson of the third Lord Henley who sent me the pedigree of his family giving the example of the kind of marriage that would provide the critical test. This I published in THE EUGENICS REVIEW.* His grandfather had married twice; one wife was a first cousin and one was unrelated. He had families by each, and those families could be traced for the second and third generations.

It was possible to show from the two previous generations that there had been no inbreeding in the families concerned. There were two great-grandchildren from the cousin marriage, twenty-three from the other marriage, a continuation of the outbreeding system. Armed with this information I appealed for other examples throughout the world, and got sixteen different families in which the same kind of test could be applied, and it is part of these results I now want to summarize. I am giving the total number of children, grandchildren and great-grandchildren.

	COUSIN MARRIAGES			UNRELATED MARRIAGES			INCREASE
	c.	gc.	ggc.	c.	gc.	ggc.	
Outbred families 5 marriages	17	7	5	12	20	45	0·3/3·7
Intermediate families 3 marriages	7	10	13	8	8	16	1·9/2·0
Inbred families 4 marriages	15	27	61	12	13	22	4·1/1·8

The unrelated marriage in the outbred family is the continuation of the normal system of breeding, which gives the 3·7 increase we expect under normal circumstances. The inbred system, the cousin marriage continuing the inbred habit of mating, gives the increase of 4·1. On the other hand the two systems which represent the break with the past also break the fertility.

Now there seems evidence of something I

* 1958. 50, 177.

had not dared to consider, because it touches a problem which has baffled people for a very long time, evidence of infertility following wide crosses in man. When I say "wide crosses" I mean race crosses. This is the first evidence I know (and I should like to know of any other) of a depreciation of fertility following outbreeding in an inbred stock.

Assortative Mating and Fertility

I regard these results as substantiating my expectation, but they do much more than substantiate it. I expected, and any reasonable Mendelian might expect, that there might well be a depreciation of fertility in the first generation, but why, he might ask, should it continue in the second generation? It is overpowering in the outbred families who had cousin marriages. Why should that be?

The explanation is not at all abstruse. It is the result of assortative mating—individuals with low fertility marry spouses with low fertility. Galton's heiresses of low fertility married peers of low fertility. The peers who married heiresses were not so interested in the things which go to make fertility as the peers who did not marry heiresses. Thus it is assortative mating which can, and I think often does, lead to near extinction and sometimes actual extinction in later generations.

The effect of fertility is cumulative and the effect of infertility is cumulative. You see what an enormous scope there is for selection operating in favour of fertility in our society. People often talk as though natural selection had ceased to operate. I should call extinction by infertility a form of natural selection, and one of the most potent we have in determining the direction of evolution of our society and of all its innumerable little sub-societies.

One word about the big evolutionary implications of the inheritance of fertility and of its relation to the breeding system. Anthropologists have been puzzled, have argued incessantly and inconclusively ever since Darwin's time, as to the reason why human beings have outbreeding systems resting upon incest taboos. I say that the evidence we have of this tremendous pressure of selection in favour of fertility is enough to account for human races having developed by instinct a repugnance for incest. Only this could guarantee the habit of outbreeding recombination.

Thus man, to whom family life has restored the sedentary conditions of a plant, has been compelled to make use of a genetic system parallel to that of the incompatibility so well known in plants.

Conclusion

That is my argument. It is in line with the assumptions Darwin made but was never able to carry to a conclusion. His suggestion was that moral feelings rested upon instincts which had been derived, encouraged and developed by processes of natural selection. To me it seems that this generalisation can be taken seriously. And it can be used to put the whole problem of the evolution of society on a new footing.

REFERENCES

Darlington, C. D. 1960. Cousin marriage and the evolution of the breeding system in man. *Heredity*. **14**, 297-332.

Darlington, C. D. 1961. Introduction to Galton's *Hereditary Genius*. Collins (Fontana).